DESERT RODENT POPULATIONS:
FACTORS AFFECTING ABUNDANCE, DISTRIBUTION, AND GENETIC STRUCTURE[1]

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Abstract.— Literature concerning North American nocturnal desert rodents is reviewed to delimit current knowledge of the importance of various factors to abundance, distribution, and genetic structure. In addition, strategies for further study are suggested. *Abundance*: That increased rodent abundance often follows flushes of annual plant growth that follow favorable rains is well established. The ultimate reason for this pattern has not been established. Competition is important as well, but predation and parasitism have received little consideration. *Distribution*: Patterns of distribution have been shown to correspond to temperature, moisture, substrate, or vegetative parameters. An important question that remains is to determine the relative importance of physiological specialization vs. interspecific interactions leading to habitat specialization. *Genetic Structure*: Despite a number of studies on desert rodent systematics, little is known of the genetic structure of desert rodent populations. Behavioral, demographic, indirect genetic, and direct genetic evidence can be used to detect deviations from panmixia.

Although desert rodents have been the subject of hundreds of studies on a number of levels (e.g., physiology, behavior, population ecology, community ecology, and systematics), it is not yet feasible to make general conclusions as to the relative importance of various factors in determining the abundance, distribution, and genetic structure of populations of desert rodents. This article is designed to help remedy this problem. We consider the possible importance of each of a number of factors, reviewing the relevant literature to determine what is known at present, then suggesting ways in which the gaps in our knowledge can be filled.

With few exceptions, we have limited our treatment to the nocturnal rodents that inhabit the deserts of North America. In addition, much of our treatment concerns rodents of the family Heteromyidae, a bias that results in large part from the greater amount of work done on that group relative to other groups.

Abundance and Dynamics

Discussion of factors affecting the abundance and dynamics of desert rodent populations has, in the past, centered on the importance of food, water, and vegetation.

More recently studies have focused on interactions among rodent species. In addition to discussing these factors, we consider predation and parasitism and argue that both are worthy of study, although little evidence exists concerning their importance.

Food and Water

Perhaps the best-documented pattern of desert rodent abundance is increased population growth and reproduction following rainfall and the growth of plants, particularly annuals. This pattern has been shown to hold for many rodent species in many geographical areas (Reynolds 1958, Chew and Butterworth 1964, Beatley 1969, Bradley and Mauer 1971, Van de Graff and Balda 1973, Newsome and Corbett 1975, O'Farrell et al. 1975, Reichman and Van de Graff 1975, Whitford 1976, Dunigan et al. 1980, Petryszyn 1982). The exact timing of rainfall is at least as important as the total amount. Both Beatley (1974) and Petryszyn (1982), working in deserts with very different precipitation patterns, have shown that rainfall early in winter is important in germination and early growth, and rainfall in the spring is necessary for further growth and flowering.

Several hypotheses have been proposed to account for this apparent dependence of ro dent populations on plant growth; all are based primarily on reproductive responses to external factors, not on effects on survivor ship. First, Chew and Butterworth (1964) suggested that rodents may consume hormonal substances within the plants that initiate reproduction. Such a triggering mechanism has been demonstrated for microtines (Berger et al. 1981 and refs. therein). Second, Chew and Butterworth (1964) and Van de Graaff and Balda (1973) found that rodents gained weight at times of plant growth or in areas where green vegetation was present and ar gued that ingesting green vegetation im proves general body condition, enabling indi viduals to reproduce. Third, Beatley (1969), Bradley and Mauer (1971), and Reichman and Van de Graaff (1975) found an increased availability or consumption of green vegeta tion during or prior to reproduction and ar gued that water and vitamins in the plants are necessary to compensate for increased de mands during gestation and lactation. Defi ciencies in vitamins (such as A or E) can lead to sterility or fetal death (Wright 1953). Fi nally, based on the common trend that in creased growth of annuals is a prelude to in creased availability of seeds and insects, O'Farrell et al. (1975), Reichman and Van de Graaff (1975), Whitford (1976), and Dunigan et al. (1980) suggested that increased repro duction may depend on increased food availability.

The problem of distinguishing among these hypotheses can be made more tractable if we recast them to reflect requirements that are common to all animals: water, energy, and nonenergetic nutrition (simply termed *nutri tion* below; includes essential fatty acids, amino acids, vitamins, and minerals). First, the "hormonal substances" hypothesis is probably based on a proximate mechanism. Rodents should not come to rely on an exter nal cue, such as a hormonal substance, unless that cue is tied to some ultimate benefit such as water, energy, or nutrients. Second, in creased "general body condition" is probably due to the increased availability of water, energy, and/or nutrients. Finally, "increased food availability" confounds the effects of energy and nutrition. The problem, then, is

to distinguish among the relative importance of water, energy, and nutrients (all of which are more available following favorable weather conditions) in leading to population increases of desert rodents.

Several studies and observations, other than the above correlative studies that led to the formulation of these hypotheses, bear on this question. Breed (1975) showed that water deprivation resulted in reduced reproductive activity in female Australian hopping mice (*Notomys alexis*), as measured by ovarian and uterine weights and follicular development. In another laboratory experiment, Yahr and Kessler (1975) found that reproductive activi ty ceased in Mongolian gerbils (*Meriones unguiculatus*) that received lettuce only once a week but continued in control animals that received daily lettuce rations. In this study, the effect of water and nutrient availability are confounded because lettuce may contain required nutrients as well as water. Soholt (1977) found that free water intake in lactat ing *Dipodomys merriami* increased by more than 200 percent over that of non reproductive females, though gestating fe males exhibited no increase. However, be cause carrots were used as the source of free water, it is not possible to distinguish be tween the importance of water and any nu trients that carrots may contain. Further more, these experiments do not demonstrate an absolute need for free water during lacta tion because females were not actually de prived of free water; they simply showed an increase in water use.

Two studies have shown a correlation be tween the density of *Neotoma* populations and the local abundance of *Opuntia* cactus (Brown et al. 1972, Cameron and Rainey 1972, Olsen 1976), although it is unknown whether the correlation is due to increased food and water availability or to increased protection against predators (woodrats often used cactus joints in constructing nests; Brown et al. 1972). In addition, Petryszyn (1982) found that *N. albigula* densities failed to respond to a single winter of higher than average rainfall, but did respond to two con secutive good years. This can be interpreted to indicate that the abundance of annual plants (which would respond to a single good winter) does not limit woodrat populations

but the growth of perennial plants (which perhaps only respond to consecutive good years) may limit woodrat populations (Petryszyn pers. comm.).

By providing a source of supplemental water, Christian (1979a) was able to cause an increase in reproductive activity in two species and increased density in one species in a community of three species of Namib Desert rodents. The species most ecologically similar to North American heteromyids because of its superior ability to conserve water (*Desmodillus auricularis*; Christian 1979b) was little affected; Christian (1979a) argued that factors other than the availability of water determine its population size. The two species more similar to North American desert cricetids or sciurids (they are poorer at water conservation than *D. auricularis*; Christian 1979b) did respond to supplemental water, indicating that the availability of water is important in determining the abundance of these species.

Two observations indicate that availability of green matter and the water or nutrients contained therein are not a requisite for reproduction. O'Farrell et al. (1975) found that female *Perognathus parvus* sometimes remained lactating for more than a month after vegetation had dried up; vegetation may have been required for initiation of reproduction, but not for lactation. Whitford (1976) observed a population increase during a year in which there was virtually no growth of green matter.

The importance of energy or nutrients is indicated by two studies in which seeds were added to experimental plots. Addition of seeds to plots in short grass prairie caused an invasion of seed-eating *Dipodomys ordii* (Abramsky 1978). Addition of seeds to plots in the western Chihuahuan desert caused a threefold increase in numbers of the largest species at the site (*D. spectabilis*) but a slight decrease in numbers of smaller species (Brown and Munger, in preparation).

The results of the studies discussed here indicate that it is unlikely that variation in a single factor, whether it be water, energy, or nutrients, will be able to account for all situations where desert rodent population increases are correlated with bouts of rainfall.

There are several reasons for this. First, species of desert rodents may vary in their requirements. This is illustrated by Christian's (1979a) finding that three species of Namib Desert rodent responded in different ways to the addition of water. It is apparent that physiological differences among species must be considered when assessing the effects of various factors on abundance.

Second, geographical differences in the stressfulness of the environment may be important. For example, all studies that showed population responses not tied to increased water availability were carried out in relatively benign (with respect to water stress) environments: south central Washington (O'Farrell et al. 1975), Chihuahuan Desert above 1000 m elevation (Whitford 1976, Brown and Munger, in preparation), and short grass prairie (Abramsky 1978). The studies that showed an apparent reproduction dependence on free water were carried out in the more stressful lower Sonoran Desert, Mojave Desert, and Namib Desert. To resolve this problem, water and food addition experiments should be performed in the harsher lower deserts as well as in the relatively benign higher deserts.

Third, insects, whose populations often respond to increased plant growth, may provide a source of moisture for several months after annual plants have died.

Finally, although these hypotheses have been couched in terms of the effects of various factors on reproduction, these same factors are likely to affect survivorship as well. Probably because of the energetic and nutritive demands of reproduction, survivorship of breeding adults tends to be negatively associated with the degree of reproductive activity (French et al. 1974, Conley et al. 1977) and thereby negatively correlated with the amount of rain-induced plant growth (Christian 1980). Juvenile survivorship, on the other hand, should be increased by the increased availability of food and water. This pattern was found by Whitford (1976), who showed that the survivorship of young heteromyids was much lower in a year with a poor seed crop than in years with good crops. Increased juvenile survivorship may have contributed directly to increased densities shown by the studies cited above, or indirectly via

reproduction in adults: increased probability of survivorship of young during years of high plant growth and subsequent plant avail- ability may be the ultimate factor that leads adults to reproduce in those years (Reichman and Van de Graaff 1975).

As noted above, desert rodent populations appear to be strongly influenced by the growth of plants following sufficient rainfall. One might ask then whether it is necessary to even consider factors other than food and water, since the availability of water, energy, and nutrients seems to explain a large part, if not all, of the variation in desert rodent abundance. We strongly feel that other fac- tors should be considered, if only to rule them out. Below we describe a series of stud- ies on desert annual plants that illustrates the need to consider other factors.

The abundance of desert annual plants is, as mentioned above, dependent on the pat- tern and amount of rainfall. Other factors have been shown to be important as well. First, intraspecific evidence appears to limit the number of seeds that germinate (Inouye 1980). Second, large-seeded species of annual plants appear to be able to outcompete small-seeded species, but seed predators (es- pecially rodents) apparently prefer larger seeds. Rodents decrease the abundance of large-seeded species, thereby indirectly in- creasing the abundance of small-seeded spe- cies (Inouye et al. 1980). And third, if large- seeded species do attain high densities (as they do in rodent exclosures) they are subject to attack by a parasitic fungus that causes a large decrease in fecundity (Inouye 1981). With this example in mind, we proceed to consider the importance of interspecific in- teractions, predation, and parasitism in deter- mining the abundance of desert rodents.

Interspecific Interactions

A population of a given species of desert rodent does not live in the absence of other organisms. In the following section, we ad- dress the possible importance of interspecific interaction in determining the abundance of desert rodents.

For competition among species to occur, some resource must be limiting. A substantial amount of evidence, much of it indirect, ar- gues that food is limiting for many species of desert rodents, especially granivorous species. As discussed above, increases in population density follow periods of high precipitation and seed production (Reynolds 1958, Beatley 1969, 1976, French et al. 1974, O'Farrell et al. 1975, Whitford 1976, Dunigan et al. 1980, Petryzsyn 1982), and invasions or population increases of seed-eating rodents follow the addition of seeds (Abramsky 1978, Brown and Munger, in preparation). In addition, den- sities of seed-eating rodents increased in re- sponse to the removal of ants (Brown and Davidson 1979) and, along a geographic gradient of increasing precipitation and pro- ductivity, population density, biomass, and species diversity of seed-eating rodents tend to increase (Brown 1973, 1975). Furthermore, woodrat populations appear to be limited by the amount of green matter available to them (Brown et al. 1972, Cameron and Rainey 1972, Olsen 1976).

A number of studies indicate the probable importance of rodent-rodent interactions. Cameron (1971) concluded that, where the two species are sympatric, *Neotoma fuscipes* excludes *N. lepida* from their preferred food plant. Frye (in press) showed experimentally that *Dipodomys merriami* were excluded from seed resources near the mounds of the larger *D. spectabilis*. A number of authors have shown that desert rodents differentially utilize microhabitats (Brown and Lieberman 1973, Brown 1973, 1975, Lemen and Rosenz- weig 1978, Price 1978a, Wondolleck 1978) or habitats (Rosenzweig 1973, Schroeder and Rosenzweig 1975, Hoover et al. 1977, War- ren 1979). That this differential use is caused by interspecific interactions is indicated by studies that have shown a shift in micro- habitat use as a result of experimental remov- al (Price 1978a, Wondolleck 1978) or a natu- ral lack (Larsen 1978) of putative competitor species. In addition, although food may not be the basis of the response, the granivorous *D. ordii* expanded its microhabitat use in re- sponse to removal of the omnivore *Onych- omys leucogaster* (Rebar and Conley, in prep- aration). Exclusion of one species by another from a preferred resource or microhabitat can potentially lead to a reduction in popu- lation size for the former species.

Removal experiments that measure numerical response are even stronger evidence of the importance of interspecific interaction. Unfortunately, few such studies have been done. Schroeder and Rosenzweig (1975) performed reciprocal removals of *D. ordii* and *D. merriami* but found that neither species responded to removal of the other. Munger and Brown (1981) found a 3.5-fold increase in the population density of small granivorous rodents following the absolute removal of three species of *Dipodomys*. In a third study, Eidemiller (1982) performed reciprocal removals of the herbivorous *Neotoma lepida* and the granivorous *Perognathus fallax*. Three species of omnivorous *Peromyscus* responded with a twofold increase to *N. lepida* removal but failed to respond to *P. fallax* removal. The response of *N. lepida* to the removal of *P. fallax* and the reciprocal response were minor.

To further assess the importance of inter-specific interactions, more removal experiments must be performed. To be of value, these experiments must be properly replicated; a surprising number of studies appearing in the literature lack experimental replication (Hayne 1975).

A number of questions can be addressed with these studies. First, how general are the results of the experiments discussed here? Another, is the result affected by the identity of the species studied, by the habitat in which the study was conducted, by the presence of other competitor or predator species (which may be affected by historical factors such as colonization events or ecological bottlenecks), by the season in which the study was performed, or by the temporal pattern of resource availability? One tenuous pattern that emerges is that similar-sized species failed to respond to removals (Schroeder and Rosenzweig 1975), whereas dissimilar-sized species responded to removals (Munger and Brown 1981; although this was not true in all cases for Eidemiller 1982). Such a generalization contradicts other studies that suggest that the intensity of pair-wise interactions among granivorous rodents increases with body-size similarity (Brown 1973, 1975, Brown and Lieberman 1973, Mares and Williams 1975, Bowers and Brown 1982). As discussed by Schroder and Rosenzweig (1975), it

may be that the interaction between similar-sized species has been sufficient, over evolutionary time, to discourage utilization of a common set of resources (see discussion under habitat selection).

Second, by examining the bases of these interactions in detail, a great deal can be learned about their impact on population dynamics. For what resource are these rodents competing? Does the interaction involve exploitation or interference competition?

Predation

The most direct way to assess the effect of predation on desert rodent populations is to remove predators then measure any response there may be in the abundance and distribution of the rodents. Much information about predator-prey interactions can also be gathered through detailed observations of population numbers, distribution, and behaviors of predators and prey as shown by what is undoubtedly the most complete study of the effects of predation on the population dynamics of a small mammal: the work of Errington (1943, 1946) on muskrats (*Ondatra zibethica*) and their primary predator, mink (*Mustela vison*). Unfortunately, no study approaching this quality has been performed on desert rodents and their predators (perhaps because much of their activity is nocturnal); therefore, we must rely primarily on indirect evidence in this section.

Errington's work illustrates a further point: the scale on which the results are viewed drastically affects the interpretation. Although large numbers of muskrats are killed by mink and other predators, Errington (1946, 1956) argued that predation is overrated as a factor controlling muskrat populations. Instead, he argued that population size is controlled by the availability of territories; predation primarily affects the surplus individuals (those without territories) of a population and is only one of a number of factors that affect surplus animals of the population. Although he may be correct that territory number limits population numbers and density within a marsh, it is predation that makes areas outside the marsh unsafe, ultimately limiting the number of territories that can be safely occupied. If it is the presence of

mink that prevents muskrats from success- fully colonizing areas near the marsh (where food and water are accessible), then pre- dation would have to be considered to be a factor important in limiting distribution and therefore total population size of muskrats. On a within-habitat scale, predation appears to be unimportant. On a between-habitat scale, it may contribute substantially to the limitation of the population.

Errington's studies illustrate both a direct effect (increased death rate: those individuals that do not possess safe territories are often killed) and an indirect effect (habitat selec- tion: given a choice, muskrats will selectively live in habitats that are relatively safe) of predation on abundance and distribution. In desert rodent populations, direct effects of predation have yet to be demonstrated, though a number of studies have shown that desert rodents are, in fact, killed by a number of predators, e.g., owls, carnivores, and snakes (French et al. 1967, Egoscue 1962, Webster and Webster 1971, Lay 1974, Ryck- man et al. 1981, Munger, pers. obs., Jones, pers. obs.).

French et al. (1967) tried to estimate the direct effect of kit fox (*Vulpes macrotis*) pre- dation on the survivorship of desert rodents by comparing longevity (which included loss by emigration) in unfenced populations (sub- ject to losses by emigration and predation by kit foxes and other predators such as snakes) with longevity in fenced populations (from which kit foxes were excluded and out of which emigration was not possible). The ef- fect of emigration (measured in another study at 25 percent per year) was subtracted from the sum of all effects on longevity of the fenced population. They concluded that kit fox predation was unimportant in affecting longevity, though predation by other pre- dators may have been important. Although this approach was novel, it suffers an impor- tant flaw: the calculations of French et al. (1967) are overly sensitive to the values en- tered into their equations. For example, a de- crease in the emigration value used from 25 to 24 percent results in a sixfold increase in the apparent importance of kit fox predation. Since no confidence intervals are given for any of their values, the exact importance of this sensitivity is unknown.

The effect of other factors, such as produc- tivity, competition, and parasitism, may be manifest primarily through predation. It is likely that a decrease in productivity, an in- crease in competition, and an increase in par- asitic load will all require rodents to spend more time foraging to meet energetic re- quirements. This, in turn, will increase their exposure to predators, and potentially di- rectly affect abundance.

It is somewhat easier to examine indirect effects of predation because these often in- volve morphologies and behaviors that may be more easily studied than density effects. Behaviors and morphologies that lead to a re- duction in the probability of being killed should evolve in desert rodents. If these be- haviors and/or morphologies are costly or re- duce resources available to a population (for example by restricting foraging to certain mi- crohabitats), then predation can potentially have an indirect effect of lowering popu- lation size.

Several studies indicate that one indirect effect involves microhabitat selection. Quad- rupedal desert rodents forage substantially more under and around bushes than out in the open (Brown and Lieberman 1973, Ro- senzweig 1973, Price 1978a, Wondolleck 1978, Thompson 1982a). Though this may be due in part to differences in resource avail- ability (Reichman 1975, Brown et al. 1979a), a number of authors have argued that these rodents favor bush microhabitats to avoid at- tacks by visually oriented predators (Rosen- zweig 1973, O'Dowd and Hay 1980, Thomp- son 1982a, Kotler, in press).

Four studies provide experimental evi- dence consistent with the notion that pre- dation importantly affects microhabitat selec- tion. Thompson (1982b) was able to increase the density of quadrupedal rodents in an area by constructing artificial shelters in the open spaces between bushes. By increasing the amount of cover available, the shelters may have allowed the rodents to utilize areas they previously avoided, resulting in an increased population size. Because measures of seed density failed to show any effect by the shel- ters on resource distribution, it is unlikely that the density increase was caused by changes in the resource base. Rosenzweig (1973) decreased the number of *Perognathus*

penicillatus captured by experimentally re- moving shrubby vegetation. The rapidity of the response indicates that it is unlikely that the rodents were responding to a change in resources. O'Dowd and Hay (1980) showed that the probability that desert rodents ex- ploit artificial seed patches varies with the distance of those seeds to the nearest bush (presumably a measure of the danger of being preyed upon) but not with the quality of those patches.

The results of these three studies are open to an alternate explanation. The ultimate rea- son that quadrupedal rodents prefer bushy microhabitats may be that bushes have been associated (over evolutionary time) with par- ticular resource distributions and are present- ly used by rodents as proximate cues to favor- able resource patches. In the studies of Rosenzweig (1973) and Thompson (1982b), the rodents may have responded to changes in the proximate cue even though the ulti- mate factor remained unchanged. The oppo- site may have occurred in the study of O'Dowd and Hay (1980): the rodents may have failed to respond to changes in the ulti- mate factor (seeds) because there was no change in the proximate cue.

By manipulating a factor other than micro- habitat, Kotler (in press) avoided this prob- lem. He reasoned that, because many pred- ators of nocturnal desert rodents rely on visual cues, the rodents should use the amount of illumination in the environment to assess their risk of being preyed upon. Using artificial light sources, Kotler experimentally increased the amount of illumination, causing four of the six species at his study site to re- duce their use of open habitats, indicating that the utilization of microhabitats by these species is sensitive to the risk of being preyed upon. It is interesting to note that one spe- cies, *D. deserti,* responded to increased light only when resources in bushy microhabitats were augmented, indicating that resource availability and risk of predation may inter- act in affecting behavior. The two remaining species made little use of open microhabitats prior to experimental treatment; a decrease in the use of open areas by these species would therefore be difficult to cause or detect.

Several other studies indicate that pre- dation may be an important selective force in desert rodents. First, timing of foraging activ- ity is sensitive to moonlight; presumably in- creased light increases the probability of being preyed upon (Lockard and Owings 1974, Rosenzweig 1974, Kaufman and Kauf- man 1982). Second, individuals of the island- dwelling *Neotoma lepida latirostra* spend more time away from the nest and travel in more open areas than their mainland counterparts, presumably due to a lack of predators on the island (Vaughan and Schwartz 1980). Third, desert rodents in sev- eral families possess auditory and locomotory specializations (Bartholomew and Caswell 1951, Webster 1962, Webster and Webster 1975, Lay 1972) that have shown to be im- portant in aiding these rodents in avoiding attacks of predators (Webster and Webster 1971). These rodents also possess pelages which match the substrate on which they oc- cur (Dice and Blossom 1973). It should be noted, however, that demonstrating the im- portance of predation on the evolution of be- havioral and morphological traits does *not* demonstrate its importance in affecting abun- dance and distribution.

Obviously, much work needs to be done before the importance of predation can be assessed. Indirect studies need to be bolstered by determining whether the ultimate factor responsible for such behaviors as avoidance of open microhabitats is based on resource distribution or predator avoidance. This task will prove difficult if behaviors are inflexibly tied to proximate cues. Studies that measure the direct effect of predation on abundance and local distribution should be attempted as well, perhaps using island systems (cf. Vaughan and Schwartz 1980) or areas where predators have been subjected to control programs.

Parasitism

The role that parasitism may play in af- fecting the abundance and distribution of desert rodents has been given little consid- eration, even in comparison with the small amount of attention given predation. There are several reasons for this. First, antiparasite adaptations (such as immune response) are

not easily recognized and the effects of para-
sites are often indirect and subtle. Second,
because it is difficult to manipulate parasite
loads under field conditions, it is not easy to
study the importance of parasites. Third and
perhaps most important, biologists often be-
lieve that parasites have little ecological im-
portance (but see Price 1980 and Anderson
and May, 1982a). This is based on the notion
that parasites should evolve to minimize their
effect on their hosts: by damaging its host, a
parasite would supposedly reduce its chances
of reproducing.

In arguing that parasites are worthy of
consideration in the population biology of
desert rodents, we will consider two ques-
tions. First, how might parasites affect abun-
dance and distribution and, second, what is
the evidence that parasites can be important
in affecting abundance and distribution? For
this latter question, we consider a number of
systems outside desert rodents as well as re-
viewing the meager evidence pertaining to
desert rodents.

Parasites (which we consider here to in-
clude viruses through parasitic arthropods)
can affect abundance both by lowering survi-
vorship and by consuming energy that might
otherwise go to host reproduction, thereby
reducing fecundity. Anderson and May (1978,
1979, 1982b), Anderson (1978), and May and
Anderson (1978, 1979) provide excellent dis-
cussions of the dynamics of parasite and host
populations. They argue that the ability of a
parasite to regulate a host population is en-
hanced by factors that promote the stability
of the parasite-host dynamics, such as over-
dispersion of parasites, density-dependent re-
straints on the growth of parasites within
hosts, and a nonlinear relationship between
parasite burden and host death rate. They do
not mention another very important stabiliz-
ing factor: the presence of a second host spe-
cies that does not suffer pathological effects
from infection—a reservoir for the parasite
(Baltazard et al. 1952, cited in Nelson 1980).
Reservoir hosts may be especially important
in affecting distribution (see discussion
below).

If parasites are to be important in regu-
lating the abundance of the host, they must
maintain enough virulence to reduce the sur-
vivorship or fecundity of the host (the follow-

ing discussion is based on Anderson and May,
1982a).

The reproductive rate (and therefore fit-
ness) of a parasite is governed by three fac-
tors. A higher reproductive rate will result
from (all else being equal): higher probability
of infection in an uninfected host when en-
countered by an infected host (higher trans-
mission rate), lower rate at which a host re-
covers from a parasitic infection (lower
recovery rate), and lower probability that a
host dies as a result of an infection (lower
virulence). If the reproductive rate of a para-
site depended solely on its virulence, but if
virulence was not tied to the transmission
rate or recovery rate, it would be reasonable
to expect the parasite to evolve to have a
negligible effect on the host. However, these
parameters are interrelated, at least in some
systems. In the myxoma virus–rabbit system
for instance, hosts infected with more viru-
lent strains of virus had a slower recovery
rate and a higher transmission rate than hosts
infected with strains of low virulence (Ander-
son and May, 1982a). Given the character of
these interrelationships, parasites should
evolve to some intermediate rate of viru-
lence, low enough to prevent a premature
death of the host but high enough to retard
recovery and facilitate transmission. This is
what has happened in the myxoma–rabbit
system (Fenner and Ratcliff 1965, Anderson
and May, 1982a). The virus introduced was
extremely virulent; nearly 100 percent of the
infected rabbits died quickly. Eventually the
system stabilized such that the most preva-
lent viral strains were of neither very high
nor very low virulence, but somewhat inter-
mediate in their effect.

Studies of the effect of parasites on small
mammal hosts are relatively rare. In addition,
a number of these studies have questionable
worth in assessing the importance of parasites
in natural situations. First, some studies use
laboratory animals as hosts, a practice that
ignores the importance of coevolution of par-
asites and their hosts. Second, many studies
are correlative: a measure of host condition is
tied to parasite load. Such correlative studies
do not allow us to assign cause, since some
other factor, such as poor nutrition, may have
led to both poor condition and high parasite

load. Laboratory studies that utilize experi-
mental variations in parasite load will allow
us to assess the effect of parasites on survivor-
ship and fecundity. Only by performing field
studies in which parasite loads are manipu-
lated on the scale of the population will we
know if the effects of parasites on survivor-
ship and fecundity translate into actual ef-
fects of population regulation. For illustra-
tive purposes, we will list several examples of
apparent importance of parasites on de-
mographic parameters of mammals (other ex-
amples can be found in Davis and Anderson
1971, and Price 1980): Infections of *Pero-
myscus leucopus* by *Cuterebra fontinella*
(bot fly) are correlated with reduced hemato-
crit (Childs and Cosgrove 1966); delayed fe-
male maturity, delayed litter production, and
reduced male fertility (Cranford 1980); they
may also cause reduced size of reproductive
organs in subadult males, but have no dis-
cernible effect on the size of adult reproduc-
tive organs (Timm and Cook 1979). Epizoot-
ics occasionally decimate populations of
Ondatra zibethica (Errington 1954). In-
fections by lungworms (*Protostrongylus* spp.)
are thought to be very important in decreas-
ing survivorship in bighorn sheep in North
America (Forrester 1971).

What evidence exists that the abundance
of desert rodents may be affected by para-
sitism? Numerous studies have shown that
desert rodents are often infected by a number
of parasites—plague virus, nematodes, ces-
todes, spirochaetes, mites, fleas, and ticks
(Eads and Hightower 1952, Read and Mille-
man 1953, Grundman 1957, 1958, Reisen and
Best 1973, Bienek and Klikoff 1974, King and
Babero 1974, Whitaker and Wilson 1974,
O'Farrell 1975, Egoscue 1976, Garner et al.
1976, Maser and Whitaker 1980, Ryckman et
al. 1981). However, to our knowledge, very
few studies have mentioned the effects of
these parasites on their hosts. Garner et al.
(1976) indicated that *Dipodomys ordii* indi-
viduals infected with cestodes had a reduced
amount of axillary and groin fat. Several
studies of gastric parasites have noted that
the stomach of the host appears distended, ir-
ritated, or simply filled with parasites (Gar-
ner et al. 1976, Grundman 1958, King and
Barbero 1974). No study has assessed the ef-
fect of parasitism on population size.

Two strategies of study can increase our
knowledge of the importance of parasitism in
desert rodent populations. First, laboratory
studies utilizing wild rodents and their natu-
ral parasites can be used to make precise
quantitative measures of the effect of parasite
loads on parameters important to the demog-
raphy of a population. Second, field studies
should be attempted in which internal para-
site loads are manipulated by administering
the appropriate drug to a portion of a popu-
lation and external parasites are manipulated,
perhaps at burrow sites, using techniques
used to control the ectoparasites of domestic
animals (e.g., flea collars). Such studies should
yield further information on the effects of
parasitism demographic parameters and, per-
haps, on the effect of parasitism on rodent
abundance.

DISTRIBUTION

In this section, we address two basic ques-
tions. First, what factors are important in de-
fining the geographic ranges of desert ro-
dents? Second, within the range of a species,
why doesn't that species occur ubiquitously
over all habitats? That is, what factors lead to
patterns of local distribution? As will be seen,
many of the factors important in determining
abundance should also affect patterns of local
geographic distribution.

After a brief discussion of physical barriers,
we will address the importance of three
abiotic factors (temperature, moisture, and
substrate) and four biotic factors (vegetation,
competition, predation, and parasitism) to lo-
cal and geographic distribution. It is common
for two or more factors to interact in a syner-
gistic manner. In the discussion below, the
most common example of synergism is the in-
teraction of temperature, moisture, and sub-
strate to produce patterns in the distribution
of vegetation, which in turn appears to affect
the distribution of desert rodents.

Physical Barriers

Physical barriers (e.g., habitat dis-
continuities, mountain ranges, rivers) often
persist over long periods of time, are readily
discernible, and, for desert rodents, can be
put on maps (e.g., Hall 1946, Durrant 1952,

Hall and Kelson 1959, Hall 1981). In general these barriers represent both the proximate and ultimate factors that circumscribe the geographic distributions of species.

Hall (1946), Durrant (1952) and, more re cently, Brown (1973, 1975), and Brown and Lieberman (1973) noted striking differences in the composition of rodent communities in the eastern and western Great Basin desert. They suggested that eastern Great Basin desert communities are depauperate and that orographic barriers have limited certain spe cies (e.g., *D. deserti, D. merriami, Microdipodops pallidus*) to western habitats. Physical barriers often can be invoked to account for the limits of spatial distribution on at least one range boundary of many desert het eromyid, cricetid, and sciurid species in North America (Hall and Kelson 1959, Hall 1981). Besides orographic barriers, rivers ap pear to play a significant role in limiting the distribution of populations of a species. Range boundaries of *Perognathus formosus, P. spinatus, P. penicillatus, P. intermedius, Ammospermophilus leucurus*, and *A. harrisii* are partially coincident with the Colorado River. The high frequency with which phys ical barriers limit species' distributions cor roborate other empirical data that suggest that mammals are relatively poor dispersers across unsuitable habitats (Carlquist 1965; Brown 1971, 1975).

Abiotic Factors:
Temperature, Moisture, Substrate

Abiotic factors that vary in a continuous or mosaic manner are also important in circum scribing geographic ranges and affecting local distribution, although their effects are usually more subtle than those of the highly visible physical barriers just discussed. In many situations, cause and effect relation ships may be confounded by synergistic inter actions among variables and by an inability to distinguish proximate from ultimate fac tors. In the next section, we first discuss how single abiotic factors can limit distributions, then deal with the problem of synergism.

Correlations between the distribution of desert rodent species and various measures of temperature have been reported in the liter ature for many years. Sixty years ago, Grin nell (1922) suggested that temperature was

important in creating barriers to dispersal and, ultimately, could be used to account for the distribution of *Dipodomys* in California. The observations that *D. merriami* has rela tively little ability to regulate body temper ature (Dawson 1955) and that the northern extent of its distribution is coincident with the 30 F isotherm for average January tem peratures (Reynolds 1958) suggests that low winter temperatures may limit the range of this species to warm desert habitats. Gaby (1972) found that *D. merriami* (an inhabitant of low, hot deserts) and *D. ordii* (which tends to inhabit higher, cooler deserts) have inter specific differences in temperature-dependent metabolic rates that correspond to the different requirements of their ranges. In these experiments *D. ordii* was less tolerant of high temperatures than *D. merriami; D. mer riami* had a higher metabolic rate at low am bient temperatures. Unfortunately, it is un clear what role these intrinsic differences play in affecting geographic distributions. The question becomes one of cause and ef fect: are *D. merriami* populations limited to warm desert regions because they are unable to cope physiologically with colder temper atures, or are the metabolic differences be tween these kangaroo rats merely a result of local adaptation to contrasting environmental conditions?

Physiological research has long demon strated, through the study of functional adap tations, the high premiums placed on water conservation for rodents in desert habitats (Howell and Gersh 1935, Schmidt-Nielsen et al. 1948, Schmidt-Nielsen and Schmidt-Nielsen 1951). More recently, negative effect of increased ambient temperature on water balance has been elucidated (MacMillen and Christopher 1975). Beatley (1969a, 1976) noted that a species must necessarily be lim ited to areas where positive water balance (a function of interaction of temperature, avail able moisture, and the physiology of the spe cies in question) can be maintained.

Howell and Gersh (1935) first quantified the urine-concentrating capacities of *Dipodomys* and found substantial interspecific variation. That this capacity at least corre sponds to distribution is indicated by studies comparing *D. merriami* and *Dipodomys* of less arid habitats: *D. merriami* has a higher

urine-concentrating ability (comparison with *D. agilis*; Carpenter 1966) and a lower rate of body water turnover (comparison with *D. microps*; Mullen 1971).

Substrate characteristics also appear to affect distributional patterns of desert rodents. Grinnell (1922) suggested that desert rodents are limited in geographic distribution via the matching of pelage coloration with color tone of the background, though this may be a matter of local adaptation. Other studies contend that both local and geographical distributions of desert rodents are limited to those areas with soil conditions that do not inhibit the burrowing habits of a given species. *Dipodomys deserti* appears to be restricted to deep sand areas, a substrate that is conducive to the construction of large, deep burrow systems (Grinnell 1914, Hall 1946, Reynolds 1958, Roth 1978). *Dipodomys merriami* is often excluded from areas that have a surface layer of rocks, heavy clay, sulphate crust, or hard-pan because of the difficulty in digging burrows in such soil types (Vorhies and Taylor 1922, Hardy 1945, Hall 1946, Huey 1951, Reynolds 1958). In fact, Huey (1951) suggested that this was the main factor controlling the geographic distribution of *D. merriami* below 4500 feet in western North America.

The complex nature of physiological interactions (primarily through the dissipation of heat and conservation of water) with burrow environments suggests that local distributions may be affected by soil type (Gaby 1972, Hoover 1973) as well as the potential for burrow ventilation via surface winds (Kay and Whitford 1978). Such speculation is supported by some novel work that employs physiological and behavioral data to account for the distribution of two species of *Perognathus* in New Mexico. This work (Hoover et al. 1977) suggests that *P. intermedius* can tolerate a wide range of burrow microclimates but is behaviorally excluded by *P. penicillatus* from substrates that have a high heat buffering capacity (the preferred burrow sites of *P. penicillatus*). If *P. penicillatus* can tolerate only a small range of burrow microclimates and is behaviorally dominant to *P. intermedius*, this is an example of an included niche (Colwell and Fuentes 1975). Unfortunately, definitive experiments in which *P. penicillatus* is experimentally removed to see if *P. intermedius* is, in fact, behaviorally relegated to less-preferred habitats by *P. penicillatus* were not performed. Nevertheless, the data strongly suggest that physiological differences between these species mediate the interspecific interactions that determine the local distributions of these species.

More recently, hypotheses that focus on interspecific interactions and differential foraging behaviors have been invoked to account for patterns of substrate philopatry in some rodent species. Reichman and Oberstein (1977) and Price (1978b) have suggested that divergent body sizes and morphologies of heteromyid species reflect adaptations for exploiting different seed dispersions. Seed density and dispersion appear to be affected by microtopography and soil structure (Reichman and Oberstein 1977, Bowers 1979, 1982). Areas with fine substrates permit the accumulation of dense seed aggregations by trapping windblown seeds in depressions, whereas on substrates consisting of larger soil particles, seeds are trapped individually. Because of their larger size and saltatorial locomotion, *Dipodomys* are thought to specialize on the exploitation of seed clumps that provide large energy returns per unit time. Therefore, the distribution of *Dipodomys* should be coincident with fine substrates. In contrast, the smaller, quadrupedal *Perognathus* are thought to forage for more dispersed (individual) seeds and, consequently, should prefer areas with larger soil particle sizes. Differential substrate utilization between these genera has been documented at the local habitat level (Wondolleck 1978, Bowers 1979); there is no *a priori* reason why the same mechanism might not be working to affect geographical distributional patterns as well.

Vegetation

Possibly the greatest effect of temperature, moisture, and substrate is a synergistic one, affecting the local patterns of vegetative structure and the distribution of certain plant species. Dice and Blossom (1937) suggested that the physiognomy of the vegetation was

an important factor in determining the distribution of desert rodent species. More recently, positive relationships between annual precipitation and perennial plant species diversity, density and size (Beatley 1969, Brown 1973, Hafner 1977), as well as perennial and annual seed standing crop (Lieberman 1974) have been established. That *D. merriami* is limited in geographic distribution to areas receiving less than 25 cm of annual precipitation (Reynolds 1958) and prefers habitats of little vegetative cover (Hall 1946, Lidicker 1960, Brown and Lieberman 1973, Rosenzweig 1973, Schroder and Rosenzweig 1975) suggest an indirect effect of moisture on limiting habitat characteristics for some species. By comparison, *D. ordii* is apparently limited in distribution to more grassy habitats that have an annual precipitation of more than 25 cm (Reynolds 1958, Schroder and Rosenzweig 1975). A similar relationship may occur on a geographic scale: *D. merriami* has expanded its geographic range to include overgrazed grassland (now desert scrub) habitats that once were more typical of *D. ordii* habitats (Reynolds 1958).

Precipitation, through its effect on the quantity of available food (seed) resources, may also affect the geographical distribution of some desert rodent species. Frye (pers. comm.) found that most species of large ($>$ 100 g) *Dipodomys* species are restricted to those areas that predictably receive substantial annual precipitation. It is likely that the relatively large amount of food resources required by rodents of large body size coupled with the constraints of finite foraging areas limits large species to more productive areas. A potential exception to this pattern is *D. deserti*, which often occurs in areas of the Mojave and southwestern Great Basin deserts that receive little precipitation. Although the total amount of resources produced in these areas is probably comparatively small, *D. deserti* is restricted to sand-dune habitats, which should be richer than surrounding habitats. This is because food resources will be concentrated in dune areas on two different scales by the action of surface winds. First, the same wind patterns that transport sand from the surrounding valley and concentrate it into dunes will transport seeds to dune areas as well. Second, on

the dunes themselves, seeds will tend to accumulate in depressions, thereby further concentrating the resource, making it more efficient for kangaroo rats to harvest.

The interaction of climatic and substrate variables affect the distribution of certain plant species or types (e.g., the associations of Shelford 1913) to which, in turn, are closely tied the distribution of some desert rodents. For example, it is well documented that the distribution of *D. microps* is coincident with the distribution of chenopods of the genus *Atriplex* (Grinnell 1933, Jorgensen 1963, Kenagy 1972a, b), upon which it is physiologically and morphologically adapted to feed (Kenagy 1972a, b; but see Csuti 1979). *Atriplex*, in turn, is usually limited to alkali flats surrounding dry basins of Pleistocene Lakes (Hall and Dale 1939, Munz and Keck 1959).

Field observations (Hall 1946, Cameron 1971, Brown et al. 1972, Cameron and Rainey 1972, Olsen 1975) have documented relationships between the presence of cricetid rodents and succulent desert vegetation. It is likely that this pattern results from the need of some species of *Peromyscus* and *Neotoma* to consume succulent vegetation to maintain positive water balance (Olsen 1975).

Interspecific Interactions

Comparative physiological data do not always account for differences in the local distribution of closely related species, and other causal and effect mechanisms must be invoked. Lee (1963), in an investigation of the physiological adaptations of *N. lepida* and *N. fuscipes* to arid and semiarid habitats, found no physiological bases for the observed differences in local distribution where the species ranges overlap. A study focusing on the competitive relationship of these species in the Mojave Desert of southeastern California found that these species are distinctly separated in most aspects of the habitat (Cameron 1971). Dietary studies, however, revealed that, when allopatric, both *N. fuscipes* and *N. lepida* prefer a common food plant (*Quercus turbinella*), whereas *N. lepida* switches to a less preferred species (*Juniperus californica*) when sympatric with *N. fuscipes*. An investigation of behavioral interactions

(Cameron 1971) suggested that *N. fuscipes* is dominant over *N. lepida*, relegating the latter to areas of low *Quercus* density, and controlling the preferred food resource via habitat selection and defense. Such data support the premise that interspecific competition for limited food resources affects patterns of local distribution.

The differential occurrence of *Dipodomys* and *Perognathus* in different, but contiguous, microhabitats has been documented by numerous studies focusing on the local distribution of these genera. This body of data represents the best-documented pattern of habitat use by desert rodents. *Perognathus* tend to inhabit areas of high vegetation cover (Arnold 1942, Hall 1946, Reynolds and Haskel 1949, Reynolds 1950, Rosenzweig and Winakur 1969, Feldhammer 1979, Brown and Lieberman 1973, Rosenzweig 1973, Price 1978a, Wondolleck 1978) and coarse substrate types (Hardy 1945, Hall 1946, Rosenzweig and Winakur 1969, Brown 1975, Hoover et al. 1977, Wondolleck 1978). In contrast, *Dipodomys*, on a local scale, tend to be found in more open microhabitats with finer substrate (Hall 1946, Lidicker 1960, Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Wondolleck 1978, Price 1978a; for a complete review, see Brown et al. 1979b; but see Thompson 1982a).

In the section on abundance, we briefly discussed two mechanisms, based on competition and predation, that have been hypothesized to account for differential utilization of microhabitats by *Dipodomys* and *Perognathus*. The predation hypothesis is based on the early observations that *Dipodomys* is better adapted to avoid predation, via locomotory (Bartholomew and Caswell 1951) and auditory (Webster 1962) specializations, when compared with the more quadrupedal *Perognathus* (although *Perognathus* was subsequently shown to share most of the auditory specializations found in *Dipodomys*; Webster and Webster 1975). Consequently, *Perognathus* are thought to occupy areas of high vegetative cover mainly as a result of predation pressure that covaries with local vegetative physiognomy (Rosenzweig 1973, Thompson 1982a). Even though recent work of Thompson (1982a) has demonstrated that *Dipodomys* also use areas of high vegetative cover, perhaps as a refuge from predation, it is thought that saltatorial kangaroo rats use open, poorly vegetated areas to a significant extent in the exploitation of food resources. The experimental work of Thompson (1982b), O'Dowd and Hay (1980), and Kotler (in press) provides evidence that predation is important in determining microhabitat use.

However, predation is not the sole factor influencing microhabitat use. If predation alone affects the differential use of microhabitats and habitats by *Perognathus* and *Dipodomys*, the experimental removals of *Dipodomys* by Wondolleck (1978) and Price (1978a) should not have caused shift in microhabitat use by *Perognathus*. In all probability, properties of the resource base that vary according to habitat microtopography interact with locomotory differences in foraging of *Dipodomys* and *Perognathus* to help produce the observed differences in habitats utilized. The competition hypothesis couches patterns of habitat use in terms of the ability of a species to exploit a resource base that varies on a spatial scale. But there are several variations on this general theme, and even the mode of competition (e.g., exploitation vs. interference) has been a subject of much discussion.

Much evidence suggests that desert granivorous rodents subdivide seed resources by exploiting different seed dispersions. As discussed above, seed density and dispersion appear to be influenced by microtopography and vegetative structure (Reichman and Oberstein 1977). Consequently, it is hypothesized that the microhabitat affinities shown by desert rodents may exist because microhabitats differ in the degree to which they contain clumped seeds. Large saltatorial *Dipodomys* forage mainly in open, vegetation-free habitats where windblown seeds accumulate in depressions or adjacent to objects acting as windbreaks (Reichman and Oberstein 1977, Bowers 1982). Thus, bipedal kangaroo rats are thought to forage from seed clump to seed clump, spending little time in the interspersed seed-poor areas (but see Frye and Rosenzweig 1980). By contrast, *Perognathus* and other quadrupeds forage under bushes (Brown and Lieberman 1973, Rosenzweig et al. 1975, Price 1978a), where seeds are more uniformly distributed.

Although such a scheme is supported by both theoretical (Reichman 1980) and empirical (see Brown et al. 1979b for a review) data, the actual mechanisms resulting in spatial segregation of *Dipodomys* and *Perognathus* on a local level are unclear. In particular, do *Dipodomys* use aggression to competitively exclude *Perognathus* from the seed-rich, open areas as suggested by Hutto (1978) and Trombulak and Kenagy (1980), or are the patterns of microhabitat use merely the result of more proficient exploitation of seed clumps by *Dipodomys* relative to *Perognathus* (Reichman and Oberstein 1977, Wondolleck 1978, Price 1978b)?

Congdon (1974) reported an instance where interspecific aggression of *D. deserti* toward *D. merriami* appeared to be dependent on the amount of available resources. In periods of low resource availability, *D. merriami* and *D. deserti* cooccurred in habitats with sand substrates, but when the resource base was augmented, indirectly, by an intense summer storm, *D. merriami* moved into nonsandy habitats, presumably to avoid the aggressively dominant *D. deserti* (Congdon 1974). This pattern may result from several factors. First, resources may have become dense enough following the storm to become economically defensible (Brown 1964) by *D. deserti*. Second, increased resource availability may have allowed *D. deserti* to spend less time foraging and more time engaged in aggressive interactions (see Caraco 1979).

Although instances of aggression in desert rodents have been reported many times (Hall 1946, Eisenberg 1963, Christopher 1973, Kenagy 1976, Blaustein and Risser 1976, Hutto 1978, Trombulak and Kenagy 1980), its role in determining local distributions is unclear. In most cases, the appropriate experiments have not been done (but see Frye, in press). In fact, some authors (Brown and Lieberman 1973, Brown et al. 1979, Bowers and Brown 1982) contend that for granivorous desert rodents it is very rare that the distribution of resources is sufficiently dense for interspecific aggression to be an economically feasible strategy.

Interspecific interactions that affect patterns of habitat use, on a local scale (Rosenzweig et al. 1975, Price 1978a, Brown et al. 1979b), might also play a role in limiting the geographic distributions of certain rodent species. Bowers and Brown (1982) found that those rodent species that *a priori* were most likely to compete (e.g., similar-sized species of the granivore guild) overlapped less in their geographic ranges and cooccur less often in local communities than a null model predicted. In contrast, overlaps between and cooccurrences of pairs with different trophic affinities (e.g., interguild comparisons) did not differ from the random model.

Body Size

Body-size, *per se,* may also play a role in determining the distribution of desert rodent species by affecting the way rodents use certain resources. Grinnell (1914) and Hall (1946) noted that an intermediate-sized heteromyid, *D. merriami,* was found in nearly every desert habitat, whereas the larger *D. deserti* was more restricted in habitat. From this pattern Grinnell (1914) concluded that larger species usually have more restricted habitat utilization patterns and more circumscribed geographic ranges than their smaller relatives. More recently, Mares and Williams (1977) reported the result that intermediate-sized species of *Perognathus* and *Dipodomys* occupy the northern and eastern range limits of the family, whereas, in the center of heteromyid diversity, an array of smaller and larger species are syntopic with intermediate-sized species. Bowers (in preparation) investigated the relationship between geographic range and body size for 46 heteromyid species and suggested that body size is an important factor in affecting the extent of a species distribution. Intermediate and very small species are characterized by having large distributions, but small and large heteromyids have relatively small ranges. As many economic, physiologic, and behavioral characteristics covary with body size (Eisenberg 1963, Rosenzweig and Sterner 1970, French 1976, Reichman and Brown 1979), it is difficult to attach cause and effect relationships between certain biological properties and geographic range. However, patterns of resource use and the propensity of a species to enter food-induced torpor, both of which change with body size (Rosenzweig and Sterner 1970, Brown and Lieberman 1973, Mares

and Williams 1977, Reichman and Brown 1979), appear to be of particular importance in the determination of geographic distribution.

Hypotheses regarding geographic distribution are almost impossible to test via manipulation. However, it seems plausible that many of the ecological factors important in affecting local distribution should also affect the extent of the geographical distribution of a species and, therefore, that geographic distribution can be studied, via inference, through studies at the local level. At best, the projection of locally studied factors to explain large scale patterns is myopic. However, such an approach has been employed in other systems with apparent success (see Glazier 1980, Reaka 1980, Brown 1981).

Habitat Selection

Throughout our discussion of distribution, we have given many examples of habitat or microhabitat affinity. An important problem that remains is to determine whether these affinities are completely due to physiological or physical limitation (which has often been implicit in our discussion, especially of abiotic factors), or whether these affinities result at least in part from habitat selection originating from competitive interactions. Rosenzweig (1979, 1981) has developed models of competition-based habitat selection that can be illustrated as follows. Imagine a species, A, that prefers habitat type a over a different type, b, perhaps because it is more efficient at harvesting resources in a. At low densities, all A will be found in habitat a. As the density of A increases, however, the fitness of individual A in habitat a will gradually decrease (because of resource degradation); eventually, habitat a will be degraded to a point where a and b are equal in quality. At this point, A should inhabit b as well as a; an observer would detect no habitat affinity (though a difference in density could exist). Now introduce species B, which prefers habitat b because it is more efficient at harvesting resources there. Because they prefer b over a, B will tend to degrade habitat b, reducing the fitness of A on b, leading A to inhabit only habitat a.

Such competition-based habitat selection neither requires nor precludes interspecific aggression. Furthermore, habitat selection may be dependent on contemporary interactions or, if interactions occur over a very long time, species may evolve inflexible behavioral, morphological, or physiological adaptations that can enforce habitat selection even in the temporary absence of the competitor species. The evolution of inflexible habitat selection was invoked by Shroeder and Rosenzweig (1975) to explain the result that reciprocal removals of $D.$ $merriami$ and $D.$ $ordii$ failed to result in either a wider range of habitats used or density change in the target species when the congener was absent.

How can it be determined if a specific case of affinity for a certain type of substrate or vegetation results from competition-based habitat selection? If habitat selection is based on contemporary interactions, removal experiments (as we called for in the $Perognathus$ $intermedius$–$P.$ $penicillatus$ system) should suffice. If, on the other hand, habitat selection has evolved to inflexibility, then simple removal experiments will not distinguish between competition-based habitat selection and a complete lack of competition: no response would be expected in either case. Study of "natural experiments" is then called for. If a species expands its use of habitats in geographic areas where the putative competitor is absent, then the contention that competition is important in causing habitat selection is supported.

Predation and Parasitism

Distribution may also be affected by predation and parasitism. The probability of being preyed upon may be so high in certain habitats that some species are either exterminated in those areas or individuals are unwilling to enter them. Although there are no documented cases of habitat or range restriction that are directly attributable to predation, it has been speculated (Brown, pers. comm.) that the range of the kangaroo mouse, $Microdipodops$ $pallidus$, may be restricted by the presence of the sidewinder rattlesnake ($Crotalus$ $cerastes$); these two dune specialists do not appear to cooccur on

dune systems even though their ranges abut. This pattern may occur because the kangaroo mice appear to be particularly vulnerable to attacks by sidewinders (which are pit vipers); instead of hopping away when attacked by a predator (as kangaroo rats do; Webster and Webster 1971), they simply remain motion-less (Brown, pers. comm.).

Parasites may be important in determining distribution as well. Barbehenn (1969) devel-oped a hypothesis in which competitive ex-clusion of one species by another species is resisted by "germ warfare" on the part of the competitively inferior species. In the simplest scenario discussed by Barbehenn, if the inferi-or species harbors a parasite to which it has evolved resistance and if the parasite is re-stricted to certain habitats by requirements of the intermediate host or vectors, then those habitats will provide refuges for the in-ferior species; individuals of the com-petitively superior species that invade this habitat will be killed by parasites. Cornell (1974) extended this hypothesis in an attempt to explain distributional gaps between con-geners. In this case, each host species carries a strain or species of parasite (to which it is resistant) but is killed when infected by the parasite carried by the other host species. Where the ranges of these host species abut, individuals of both species would be killed by parasites carried by the other species. In both these models, the interactions between the parasite and the resistant host are relatively stable; therefore it is unlikely that reduced virulence need evolve.

One example of the effect of parasites on distributions is the contraction of the range of the moose (*Alces alces*) in the face of the expansion of the whitetail deer (*Odocoileus virginianus*) range, which is thought to be caused by meningeal worms harbored by the whitetail deer that are fatal to the moose (Price 1980). Another possible example in-volves *Peromyscus maniculatus* and *Neotoma cinerea* inhabiting lava caves in northeastern California. *Peromyscus maniculatus* harbors bubonic plague; populations of *N. cinerea* in these caves are occasionally exterminated by outbreaks of disease (Nelson and Smith 1976).

Absolutely nothing is known of the impact of parasites on the distribution of desert ro-dents. To gain this knowledge will require extensive study of host-parasite dynamics within each system considered.

Population Structure

In this section we will discuss two aspects of population structure: breeding structure (who mates with whom) and certain aspects of spatial structure, primarily home range use and dispersal. We are mainly interested in the effects of these on population genetic structure, which we define here as the way in which a population deviates from panmixia. Deviation from panmixia can have several important effects on the evolutionary dynam-ics of populations.

1. Fixation of alleles by random drift is more likely to occur with small, effective population size and discrete subpopulations, than in large panmictic populations. Drift is important in one model of evolution, em-bodied in the shifting balance theory of Wright (1977), but is unnecessary or even a hindrance for evolution in models that as-sume panmixia (Haldane 1924, Fisher 1930).

2. Localized extinctions, which are impor-tant in most scenarios of group selection (e.g., Wilson 1977, Gilpin 1975) and island bio-geography (MacArthur and Wilson 1967, Brown 1971), are more likely to occur in sub-populations that are small and discrete.

3. Demic structure and resistance to immi-gration may reduce the impact that gene flow has in maintaining species integrity and thereby make interpopulation divergence more likely (Anderson 1970; but see Baker 1981).

4. The evolution of some social and al-truistic behaviors is thought to partially de-pend on subpopulation groupings that are based on kin ties (e.g., Hamilton 1972, Sher-man 1977, Michod 1979, 1980) or possession of traits common to members of a group (Wilson 1977).

5. High variance in reproductive success can result from competition for mating op-portunities (typically among males), active choice of mates by members of one sex, or differential survival of young. Differential re-productive success among members of one or both sexes will not only lead to reduced ef-fective population size (Wright 1940, Patton and Feder 1981), but it will also lead to more

rapid evolution within populations since se-
lective pressures due to variance in reproduc-
tive success are more pronounced than when
mating is random within populations (Wilson
et al. 1975).

At least four types of evidence can be used
to study population structure: behavioral, de-
mographic, indirect genetic, and direct ge-
netic. We will treat each in turn and describe
what is known for desert rodents, covering
primarily heteromyids.

Behavioral Evidence

Behavioral evidence can be used to infer
the importance and probable effect of vari-
ous mechanisms in structuring populations.
In some desert rodents, male dominance may
play an important role in breeding structure.
There is evidence suggesting that, among
some kangaroo rats, certain males may de-
fend the burrows of females against other
males. Kenagy (1976) observed two male *D.
microps* fighting at the mound of a female,
and saw the winner copulate with the female.
Similarly, Randall (pers. comm.) observed
one *D. spectabilis* defend the mound of a fe-
male against several other males. In the
thorn-forest-inhabiting heteromyid *Liomys
salvini*, Fleming (1974) found that size was a
good predictor of dominance and that larger
males were surrounded by more potential
mates than were smaller males.

In the northern grasshopper mouse,
Onychomys leucogaster, there is some evi-
dence that males and females form at least
temporary pair bonds, a behavior that would
tend to reduce variance in male reproductive
success. First, Ruffer (1965) observed male
parental care in the laboratory. Second, Ego-
scue (1960) found that, even at low densities,
members of a male-female pair of *O. leuco-
gaster* were often caught in adjacent traps,
indicating that they lived or traveled togeth-
er. A similar pattern occurs in *Peromyscus
eremicus* (Munger, unpubl. data).

Patterns of home range overlap can also be
used to infer breeding structure. For instance,
if males defend the burrows of females, as has
been observed for *D. spectabilis* and *D. mi-
crops*, there might be little home range over-
lap between males, and the home ranges of
certain males might include the mounds of

some females exclusive of other males. On
the other hand, if males do not defend the
areas of females, one expects to find extensive
overlap between males; exclusive access to
females by certain males should be rare. This
latter pattern of home range overlap charac-
terizes *D. merriami*; male-male overlap of
home ranges is extensive and the home range
of each female is overlapped by the home
ranges of several males (O'Farrell 1980;
Jones, 1982).

Data on dispersal behavior are also useful
in understanding population structure. Dis-
persal data are lacking for most desert ro-
dents, but in those species that have been
studied there appears to be a low degree of
individual vagility. Jones (1982) measured
distances moved by juvenile *D. spectabilis*
and *D. merriami*. He was able to detect suc-
cessful dispersal moves of up to 0.9 km (15 to
20 home range diameters), yet he found that
among those juveniles surviving to reproduc-
tive maturity, less than 25 percent of *D. spec-
tabilis* and only 11 percent of *D. merriami*
dispersed to areas not adjacent to their natal
sites. Most of these cases of dispersal involved
movements of less than three home range di-
ameters. The possibility of long distance dis-
persal (>0.9 km) cannot be ruled out,
though. French et al. (1974) measured dis-
persal up to 0.9 km in *Perognathus formosus*
(whose home range diameter is less than half
that of *D. merriami*; Maza et al. 1973) and
determined that more individuals dispersed
short distances and more dispersed long dis-
tances than would be expected if individuals
simply moved to the nearest vacancy. In
other words, although most individuals made
only very short dispersal moves (as was
shown for *D. merriami* and *D. spectabilis*),
there were a few *P. formosus* individuals that
moved a great distance. The possibility that
D. merriami and *D. spectabilis* make similar
long distance moves needs to be checked by
studying dispersal in these species over at
least 40 home range diameters (2 km).

Information on the extent of dispersal in
other desert rodents is sketchy. Allred and
Beck (1963) found that the average distances
between most widely separated capture loca-
tions for each individual were greatest for
Onychomys torridus males and *Peromyscus*

maniculatus males, somewhat less for *O. tor-ridus* females, *P. maniculatus* females, and *D. merriami*, and still less for *D. microps* and *Perognathus longimembris*. Among *D. mi-crops*, for which the average distance be-tween capture locations was about 76 m, 79 percent of males (n = 183) and 87 percent of females (n = 126) ranged less than 122 m. Among *P. longimembris* most animals of both sexes ranged less than 30 m (n = 102). Such data suggest that *D. microps* and *P. long-imembris* are quite sedentary. Roberts and Packard (1973) reported that the average home range size in the Texas kangaroo rat *D. elator* was .08 ha, and that the maximum dis-tance moved between traps was 87 m for males and 109 m for females. It is not clear what portion of the movements in either study represent daily movements about the home range as opposed to dispersal or shifts in home range boundaries. To understand the effects of these movements on population genetic structure, we need to know the distri-bution of movements in terms of home range to determine what fraction of an animal's movements bring it into contact with individ-uals they do not normally encounter within their own home ranges. It is also unclear from these data which movements represent permanent shifts in home ranges vs. tempo-rary excursions out of the usual home range.

We emphasize that these sorts of behav-ioral data are, by themselves, insufficient to determine how populations are structured. There are several reasons for this. First, though some dominant males may defend fe-males, subordinate males may steal cop-ulations and thus dilute the effects of territo-rial defense. Second, the timing of mating may be crucial. An observer might see sever-al males copulating with a female, but it may be that only the male that mates with her at peak receptivity during estrus will success-fully fertilize her. Third, among heteromyids, individuals occasionally make long forays (3 to 4 home range diameters) away from their usual home ranges. Maza et al. (1973) report-ed that these long distance excursions were correlated with reproductive activity in *P. formosus*. Long-distance forays also occur in *D. merriami* and *D. microps* (Allred and Beck 1963) and in *D. spectabilis* (Jones, 1982). The actual influence of these excursions on the breeding structure of a population is un-known, but it seems that they would increase the number of female home ranges to which a given male has access. And fourth, dis-persers will have no effect on population structure unless they breed or otherwise dis-rupt the breeding structure of the residents. Liebold and Munger (in preparation) have shown that dispersing female *D. merriami* tend to be less successful at breeding than their nondispersing counterparts, indicating that their effect on population genetic struc-ture might be less than would be expected from examining dispersal behavior alone.

Demographic Evidence

Breeding structure is also partially depen-dent on demography. The number of breed-ing individuals and the variance in their life-time reproductive success may be influenced by survivorship and longevity. For example, a few individuals may survive to adulthood and live through several breeding seasons, but most individuals either do not survive to reproductive maturity or reproduce only once. In this situation, the reproductive out-put of a population is concentrated in a small number of long-lived adults. The contrasting situation is one in which longevity is nearly equal for all adults so that those individuals reaching reproductive maturity all reproduce once or twice and then die. In this case the lifetime reproductive contributions of all adults might be more nearly equal than in the former situation. Both of these age struc-tures are found in heteromyids. The latter characterizes *L. salvini*. Annual turnover is nearly complete; young are born in the spring and by the next breeding season year-lings make up nearly 100 percent of the pop-ulation (Fleming 1974). *Dipodomys spec-tabilis* appears to be an example of the other situation. Holdenreid (1957) studied a popu-lation near Santa Fe for 27 months, and stated that "the population was composed of a few well-established individuals remaining continually on the area and a much larger number of animals that remained for only a few days or months" (p. 338). In general, desert rodents tend to be long lived relative to nondesert rodents (Smith and Jorgensen 1975, Conley et al. 1976; members of some

Perognathus species may live up to five years, French et al. 1967). In most cases, however, it is unknown whether there is a high variance in survivorship that might lead to a large differential in reproductive success.

Indirect Genetic Evidence

Indirect genetic evidence concerning population structure can be gathered by determining if genotypic frequencies deviate from an expectation based on random mating. Rasmussen (1964) found a deficiency of heterozygotes of blood group loci in *Peromyscus maniculatus*, implied that inbreeding was the cause, and calculated a relatively small genetic neighborhood size of 10–75 individuals. Selander (1970) found a deficiency of heterozygotes in a population of house mice and from this inferred that the population was structured into small demes (but see Baker 1981). He strengthened his assertion by citing behavioral studies that showed an organization into families or tribes. Patton and Feder (1981) calculated F statistics (Wright 1965, Nei 1975) for populations of *Thomomys bottae*. The measure of random mating within a population (F_{IT}) can be decomposed into two parts, deviation from random mating among subpopulations (F_{ST}) and nonrandom mating within a subpopulation (F_{IS}). Patton and Feder showed a significant amount of divergence among subpopulations, but results were equivocal for within-subpopulation matings. Schwartz and Armitage (1980) similarly calculated F statistics from electrophoretic data on yellow-bellied marmots *Marmota flaviventris*. They found evidence for considerable gene flow between colonies and no evidence for inbreeding, and thus concluded that it is unlikely that evolution in these marmots is accelerated by fixation of alleles via inbreeding within colonies.

Relatively little indirect genetic evidence exists concerning the breeding structure of desert rodent populations. Studies that measure allelic diversity are typically concerned with systematics at the subspecies level or above, or with describing the amount of variation that exists in populations. The published data are usually genic, not genotypic, frequencies and values of overall heterozygosity and polymorphism; genotypic frequencies are required to detect deviations

from random mating. Furthermore, sample sizes from any one population are often too small to allow statistical tests. Finally, it is not possible to determine if the samples from any one study site are from one or several subpopulations; population structure will affect the interpretation (Patton and Feder 1981).

Two studies do provide some indirect genetic evidence concerning structure in desert rodent populations. Using a pelage character, Blair (1947) showed no deviation from random expectation within subpopulations of *Peromyscus maniculatus blandus*. In addition, there was little divergence of subpopulations from nearby (less than 5 km) subpopulations, indicating that dispersal between subpopulations does occur. More distantly separated subpopulations did diverge, however. Johnson and Selander (1970) gave diagrams showing the spatial associations of genotypes at four loci in *D. merriami*, and described two of the loci as having clumped distributions of alleles. They suggested that this pattern might indicate a low level of dispersal and some inbreeding, though no statistical test of the pattern was presented. Their findings are at least consistent with the findings of Jones (1982) for dispersal distances of *D. merriami*.

Direct Genetic Evidence

Indirect evidence yields only the knowledge that some deviation from panmixia has occurred, but does not determine which mechanism causes the deviation. This is illustrated by the findings of Patton and Feder (1981): the deviations from random mating they observed within subpopulations of gophers may not have been due to inbreeding but instead to demic structure within the subpopulation.

Direct genetic evidence, on the other hand, ties a genetic effect to the mechanism causing it. For instance, by identifying genotypes at a number of polymorphic loci for all individuals within a population, it is often possible to determine precisely what successful matings have occurred in the population. Patton and Feder (1981) used this technique to show that relatively few males of the pocket gopher *Thomomys bottae* fathered most of the young in their study area.

Hanken and Sherman (1981) used it to demonstrate multiple paternity in Belding's ground squirrel (*Spermophilus beldingi* litters. Foltz and Hoogland (1981) determined that most litters of the black-tailed prairie dog *Cynomys ludovicianus* were sired by resident males within the home coterie, indicating that coteries were the units of reproduction within the population as well as the units of social structure. Foltz (1981) also used genetic evidence to determine that female old-field mice *Peromyscus polionotus* usually mate with the same male for consecutive litters, thus demonstrating long-term monogamy in this species. As yet, there are no published studies showing direct genetic evidence of structure in desert rodent populations, but work is under way for two species, *D. spectabilis* and *D. merriami.*

Clearly, there are opportunities for more research on the structure of desert rodent populations, and what we now know suggests some interesting possibilities. One of these concerns deme size and the extent of substructuring of populations. Two lines of evidence, the description by Johnson and Selander (1970) of clumped distributions of alleles and observations by Jones (1982) of short dispersal distances, suggest a substantial demic structure in *D. merriami* populations. The extent of gene flow within populations is uncertain, though. Turnover rates are quite high in *D. merriami* (80–90 percent annually; Jones, 1982), which would tend to increase gene flow. Furthermore, we do not know the extent of long-distance dispersal (greater than 20 home range diameters), nor do we understand what role, if any, is played by excursions to areas outside the usual home range. Do individuals making these excursions find mates in areas several home range diameters from their own home range, or are they more successful at finding mates among their immediate neighbors, with whom they are possibly more familiar? Genetic studies in which marker alleles are introduced in natural populations (cf. Anderson et al. 1964, Baker 1981) would help answer these questions and would aid in determining the rate of gene flow within and among subpopulations.

Other questions concern the effects of age and breeding structure on population genetic structure. We suggested above how differences in age structure, longevity, and survivorship schedules might lead to more or less variance in lifetime reproductive success of adults. In species like *D. spectabilis,* where a few individuals live through several breeding seasons but most individuals have much shorter lifespans, a core of long-lived individuals may make a disproportionately large contribution to later generations. It would be useful to know what proportion of the breeding adults in later generations are actually descendants of these long-lived individuals. And how does reproductive success vary with age? Are older males more successful at competing for mates? This would further increase variance in male reproductive success in situations where only a small proportion of males live into their second or third breeding season. These questions are probably best pursued in long-term mark-recapture studies of natural populations combined with direct genetic determination of maternity and paternity.

Population structure in desert rodents may also be related to fluctuations in density; such periodic decreases in population size are known to occur (Beatley 1969, French et al. 1974, Whitford 1976, Petryszyn 1982). These decreases may cause genetic bottlenecks, reducing the amount of genetic diversity within subpopulations. To what extent do these decreases in density affect effective population size? Furthermore, the rate of dispersal between subpopulations may vary with density. Higher interdemic dispersal rates at peak densities might partially or completely offset the reductions in variability that possibly result from population crashes. Determining the importance of density fluctuations and interdemic dispersal for population genetic structure would require monitoring genetic makeup over large areas and over a time long enough to cover at least one, and preferably more, cycle(s) of population decline and increase.

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